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# TWO NEW SPECIES OF *PSEUDOEURYCEA* (AMPHIBIA: CAUDATA) FROM OAXACA, MEXICO

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**ABSTRACT.** *Pseudoeurycea saltator* and *P. parva* are described from the mountains of Oaxaca, in southern Mexico. These new species are small, arboreal forms that inhabit bromeliads in two widely separated areas of cloud forest on opposite sites of the Isthmus of Tehuantepec. Morphological and protein comparisons suggest that although the two new forms are similar in external morphology, they are distinct species and are only distantly related to other *Pseudoeurycea*. Discovery of these new taxa complicates interpretation of cladistic relationships among Middle American plethodontid salamanders of the genera *Pseudoeurycea*, *Ixalotriton*, and *Nyctanolis*.

**RESUMEN.** Se provee la descripción de *Pseudoeurycea saltator* y *P. parva*, de las montañas de Oaxaca, en el sur de México. Estas nuevas especies son pequeñas formas arbóreas que viven en bromelias en dos áreas ampliamente separadas de bosque nublado en lados opuestos del Istmo de Tehuantepec. Comparaciones morfológicas y de proteínas sugieren que, aunque similares en morfología externa, estas dos formas son especies diferentes, lejanamente relacionadas con otras *Pseudoeurycea*. El descubrimiento de estos nuevos taxa complica la interpretación de las relaciones cladísticas de las salamandras plethodóntidas de los géneros *Pseudoeurycea*, *Ixalotriton*, y *Nyctanolis*.

## INTRODUCTION

With 24 described species, *Pseudoeurycea* ranks second only to *Bolitoglossa* (68 species) in species diversity among the 12 neotropical genera of the salamander family Plethodontidae (Wake and Lynch, 1976; Wake and Elias, 1983). Whereas *Bolitoglossa* occurs from sea level to nearly 3,000 m elevation in humid habitats throughout the New World tropics, *Pseudoeurycea* is restricted to Mexico and Guatemala, and with few exceptions its species occur only above 1,200 m (Fig. 1). *Pseudoeurycea* can be abundant locally, but most species have limited geographic ranges. Consequently, discovery of new taxa can be expected as more mountain ranges become accessible (e.g., Regal, 1966; Bogert, 1967; Lynch *et al.*, 1983; Wake *et al.*, 1989).

Here we describe two distinctive new plethodontid species that we tentatively assign to the genus *Pseudoeurycea*. Whereas these new forms complicate the systematics of an already problematic genus (Wake and Lynch, 1976; Maxson and Wake, 1981; Elias and Wake, 1983; Wake and Elias, 1983; Wake and Johnson, 1989), they also shed new light

on the evolutionary, ecological, and biogeographic relationships among the species groups of *Pseudoeurycea*, and between that genus and its closest relatives, *Dendrotriton*, *Ixalotriton*, and *Nyctanolis*. We first describe the new species, and then discuss their relationships.

## SPECIES ACCOUNTS

### *Pseudoeurycea saltator* new species

Figure 2

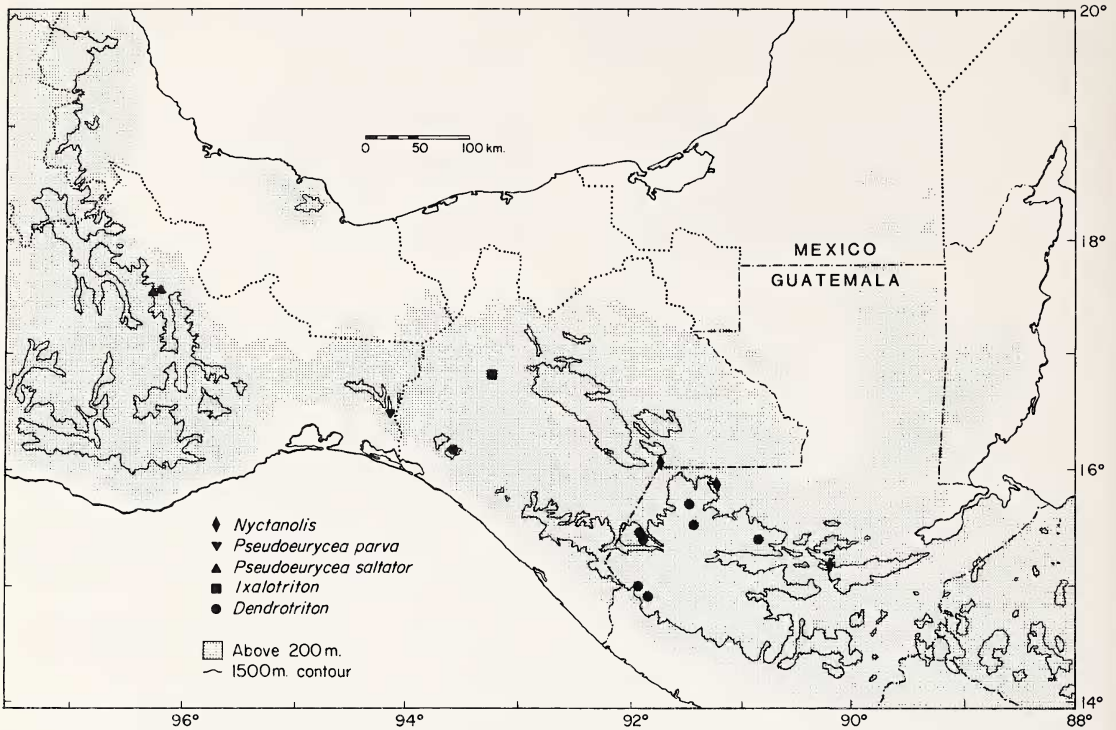
**HOLOTYPE.** MVZ 131102, an adult male collected under the bark of a fallen log in cloud forest just west of highway 175, 16 km (by road) S Vista Hermosa, Oaxaca, Mexico (1,970 m), November 21, 1974 by D.B. Wake, J.F. Lynch, and T.J. Papenfuss.

**PARATYPES.** MVZ 112227–37, 114398, 132876–80, 147259–63 (147260 is cleared and stained), 162283 (23 specimens) all within 1 km of the holotype (1,950–2,050 m) on W side of highway 175; University of Kansas (KU) 136478–99, 136512 (23 specimens) along highway 175, 4–15 km S Vista Hermosa, Oaxaca, Mexico (1,580–1,970 m); University of Texas at Arlington (UTA) A-2869–70 (2 specimens) 27 mi [= 43 km] S Valle Nacional; UTA A-3593 25 km S Valle Nacional; Natural History Museum of Los Angeles County (LACM) 137514, same data as holotype.

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1. Smithsonian Environmental Research Center, Edgewater, Maryland 21037.

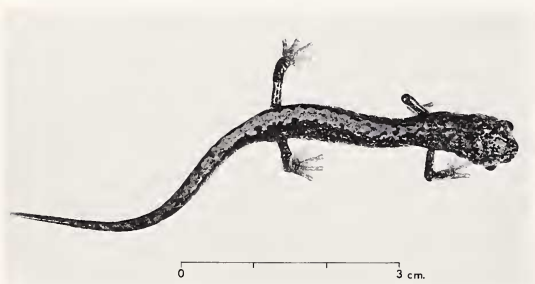
2. Museum of Vertebrate Zoology, University of California, Berkeley, California 94720; Research Associate in Herpetology, Natural History Museum of Los Angeles County, Los Angeles, California 90007.



**Figure 1.** Southern Mexico and Guatemala with the distribution indicated of the two species of *Pseudoeurycea* described in this paper. All known localities for the genera *Nyctanolis*, *Ixalotriton*, and *Dendrotriton*, which are potential relatives of these two new species, are also indicated.

**DIAGNOSIS.** *Pseudoeurycea saltator* is one of the smallest species in the genus. Standard length (SL), the distance from the snout to the posterior angle of the vent, is generally less than 45 mm (maximum = 45 mm for males, 48 mm for females;  $n = 42$ ). In its gracile external proportions and dorsally striped color pattern, *P. saltator* somewhat resembles *P. longicauda* and *P. juarezi*. The former species, which is restricted to western portions of the Transverse Volcanic Range of central Mexico (Lynch *et al.*, 1983), is much larger than *P. saltator* (males to 62 mm, females to 65 mm) and has relatively shorter limbs (combined length of the fore limb and hind limb divided by the SL averages 0.48 in *P. longicauda* vs. 0.56 in *P. saltator*). Both *P. saltator* and *P. longicauda* have long tails for the

genus (in both species, mean ratio of tail length divided by SL is greater than 1.0 in adults of average SL). Compared with *P. juarezi*, which occurs at higher elevations (2,200–2,900 m) just south of the range of *P. saltator*, the new species is smaller (median SL of the largest third of our sample = 44 mm vs. 49 mm for *P. juarezi*) and has a relatively longer tail (relative tail length = 1.05 vs. 0.96 for *P. juarezi*), more vomerine teeth (projected mean at a common SL of 45 mm = 28 vs. 23 for *P. juarezi*), and more maxillary + premaxillary teeth (projected mean at SL of 45 mm = 86 vs. 78 for *P. juarezi*). The new species also differs from *P. juarezi* in color pattern. *Pseudoeurycea saltator* has a uniformly dark gray dorsal ground color that is invariably overlain by a paler mid-dorsal stripe. A diagnostic feature of the color pattern of all adults and sub-adults is the presence of conspicuous white or cream-colored pigmentation at the tip of the tail. In contrast, the highly variable color pattern of *P. juarezi* includes a light dorsal ground color that is marked by conspicuous dark spots and a very irregular dorsal stripe (Regal, 1966); in addition, *P. juarezi* lacks a white tail tip. These two parapatric species differ greatly in electrophoretically determined traits of various proteins (see below). In external appearance, *P. saltator* is most similar to another newly discovered *Pseudoeurycea* that is described below. Diagnostic features separating these two taxa are listed in the description of the second species.



**Figure 2.** Photograph of a living *Pseudoeurycea saltator* new species (MVZ 132880), collected at the type-locality.

**MEASUREMENTS OF THE HOLOTYPE** (mm). Maximum head width, 6.0; head length (snout to gular fold), 9.2; head depth at posterior angle of jaw, 3.2; eyelid length, 2.5; eyelid width, 1.7; anterior rim of orbit to snout, 2.5; interorbital distance, 2.0; distance between vomerine teeth and parasphenoid tooth patch, 0.0; distance separating internal nares, 1.6; distance separating external nares, 2.1; snout projection beyond mandible, 0.8; snout to fore limb, 11.0; snout to anterior angle of vent, 34.1; snout to posterior angle of vent (SL), 36.8; axilla to groin, 19.1; tail length, 36.4; tail width at base, 36.4; tail depth at base, 3.0; fore limb length, 10.2; hind limb length, 11.2; width of right hand, 2.8; width of right foot, 3.7; number of premaxillary teeth, 5; number of maxillary teeth, 60; number of vomerine teeth, 28.

**COLORATION OF THE HOLOTYPE IN ALCOHOL.** The ground color is gray-black dorsally, grading to pale gray ventrally. The underside of the tail is darker than either the belly or the chin. A narrow but conspicuous mid-dorsal stripe extends from the scapular region to the tip of the tail, which is depigmented and appears white. The dorsal stripe varies in color from tan in the trunk region to gray-white on the tail. In the head region the dorsal stripe is broken into obscure flecks. Small white iridophores are scattered across the entire ventral surface but are larger and more concentrated on the chin, tail, and sides than on the belly. Coloration in life was similar, but the light iridophores were more distinct.

**VARIATION.** As in other species of *Pseudoeurycea*, the sexes of *P. saltator* overlap broadly in SL, body proportions, and coloration. However, females reach a somewhat larger overall size than do males ( $P < 0.05$ ; Mann-Whitney U-test), and the four largest individuals in our sample of 43 are females. The basic color pattern, which varies little among individuals, features a light-colored mid-dorsal stripe on a gray-black background. The dorsal stripe typically originates in the occipital or scapular region and extends posteriorly to encompass most or all of the length of the tail. The stripe varies in color from pale cream through various shades of tan, brown, or gray and is lighter posteriorly on some individuals. The margins of the dorsal stripe vary from nearly straight to ragged or scalloped. In some individuals scattered dark concentrations of melanin are present along the margins of the stripe. A consistent feature of the color pattern is the white tail tip, which is evident in all but the smallest of the available specimens. The ventral surface is paler than the dorsum and is invariably marked by small, scattered white iridophores. These iridophores are larger and more abundant in the lateral region and on the chin and tail than on the belly.

As is typical in plethodontids, there is marked ontogenetic variation in most proportional and meristic characters. Compared to juveniles (projected to a standard SL = 30 mm), adults (projected to a

standard SL = 45 mm) have more maxillary-premaxillary teeth (mean = 86 vs. 66), more vomerine teeth (mean = 28 vs. 22), relatively longer limbs (hind limb plus fore limb, divided by SL = 0.57 vs. 0.52), and relatively longer tails (tail length divided by SL = 1.05 vs. 0.81).

**OSTEOLOGY.** Information was obtained from one cleared and doubly stained male (MVZ 147260, 36.4 mm SL). The skull is compact and well ossified. The single premaxillary has a relatively broad but slender pars dentalis that bears four long, spine-like teeth; each tooth has a specialized tip consisting of a long, recurved labial cusp that extends well beyond the distinct but tiny lingual cusp and forms a minute hook-like structure. The configuration of the tooth is similar to the condition illustrated by Taylor (1941:59) for *P. unguidentis* and *P. smithi*, also Oaxacan species.

Frontal processes of the premaxilla arise independently and remain separated; these stout processes expand distally as they diverge. The processes overlap the frontal in a strong articulation, and they surround a moderately large fontanelle. The maxillaries are long and slender and bear 38 and 40 small bicuspid teeth. Septomaxillaries are absent. The nasals are relatively small, rectangular in shape, and are at most weakly articulated with the frontals and prefrontals. The well-developed prefrontal bones have areas about two-fifths those of the nasals. The nasolacrimal duct is surrounded by a distinct evacuation in the anteromedial margin of the prefrontal and a corresponding depression in the posterolateral margin of the nasal. The frontals and parietals are firmly ankylosed on the midline; there is no frontal-parietal fontanelle. A parietal "spur" is only moderately developed, and there is no ventrally directed tab. There are no crests on the otic capsules, and only one small laterally placed spine is present on one side. Vomers are weakly ankylosed for a short distance posteriorly, behind the relatively large internasal fontanelle. Preorbital processes of the vomers are long and extend beyond the body of the bone; 13–14 teeth extend beyond the lateral margins of the internal nares. The posterior vomerine tooth patches are widely separated and narrow; each contains about 65 small, bicuspid teeth. There is a well-developed, short, rod-like columella attached to the operculum.

There is an atlas, 14 trunk vertebrae (13 of them rib-bearing), 1 sacral, 2 caudosacral, and 31 caudal vertebrae. The first caudal vertebra is shorter than the second caudal or the second caudosacral and bears elongated, unbranched processes that extend sharply anteriorly. However, these processes are not especially slender or otherwise specialized as compared with the situation in other tropical plethodontids. The tail is slender. Distinct transverse processes are present on all but the small last two caudal vertebrae.

Hands and feet are typical of *Pseudoeurycea*. There is a very short, truncated tibial spur. The tarsals have the arrangement typical of the genus



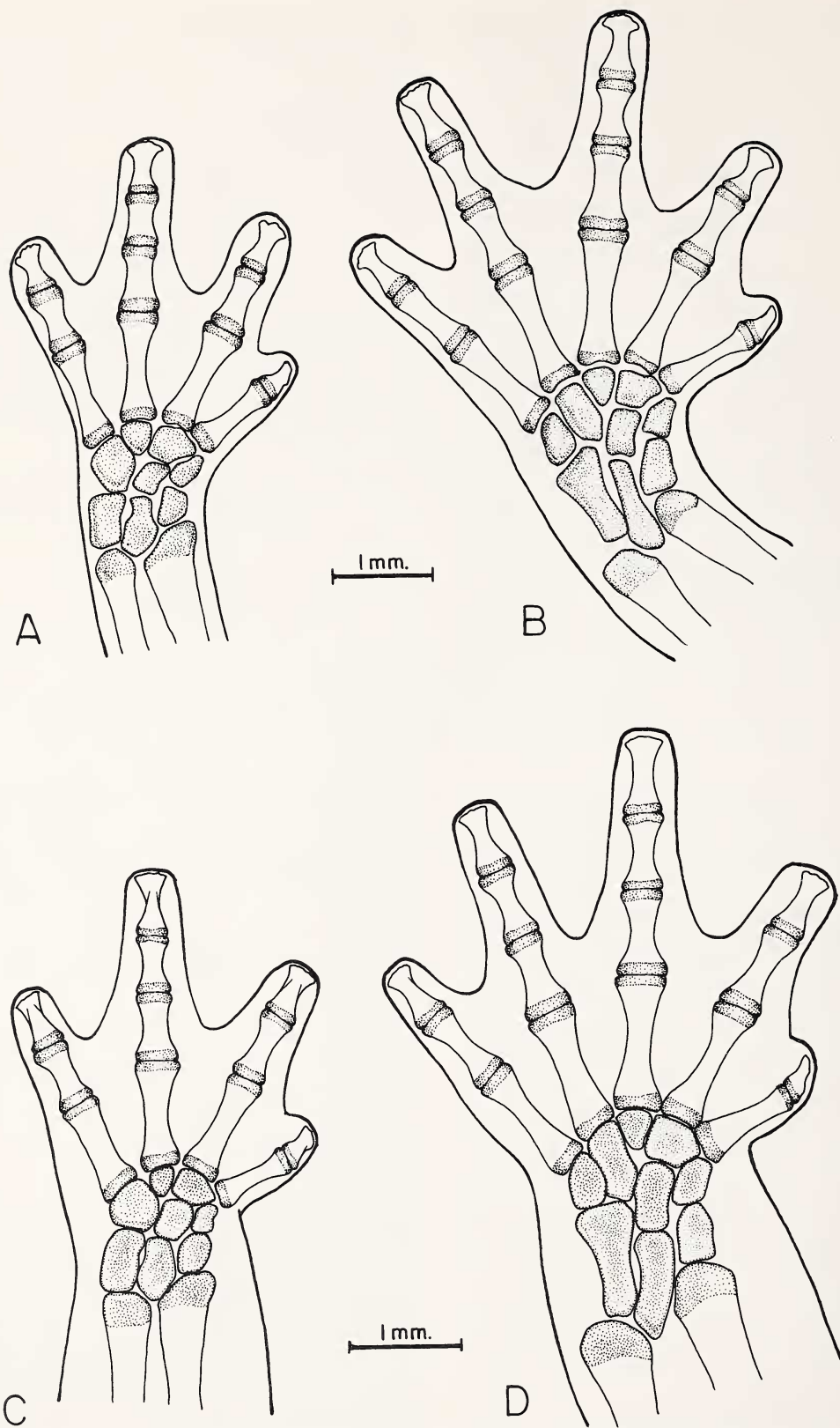


Figure 3. Drawings of the left hand (A) and left foot (B) of a paratype of *Pseudoeurycea saltator* new species (MVA 147260), and of the left hand (C) and left foot (D) of a paratype of *Pseudoeurycea parva* new species (MVZ 202294). Cartilage is stippled.



(Wake, 1966; Wake and Elias, 1983), with distal tarsal 5 being smaller than distal tarsal 4. The middle three digits of the foot are much longer than the others. Terminal phalanges are well developed and distally expanded (Fig. 3), and the distal portion is somewhat cupped. There is a small process to which the digital tendon is attached.

The hyoid apparatus is typical for the genus. No lingual cartilage is evident.

**DISTRIBUTION.** *Pseudoeurycea saltator* has been collected along a 27-km section of highway 175 that traverses the humid Caribbean-facing slope of the Sierra de Juárez, in north-central Oaxaca, Mexico (Fig. 1).

**HABITAT AND HABITS.** Most specimens have been found inside arboreal bromeliads, some as much as 8 m above the ground. A few individuals have been collected under the loose bark of downed logs. The type-locality, a steep north-facing ridge, supports a luxuriant growth of evergreen cloud forest and receives abundant precipitation even during the winter "dry" season. Extensive cloud forest is present east and west of the type-locality, but the native forest has been severely disturbed or removed by cattle ranching and coffee cultivation at the northern (*i.e.*, lower) limit of the known distribution, in the vicinity of the settlement of Vista Hermosa.

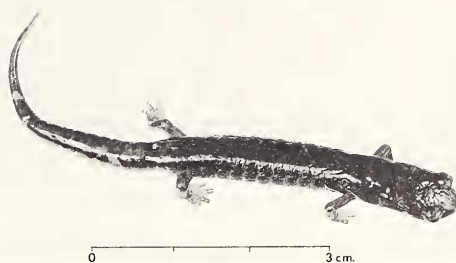
Amphibians associated with *P. saltator* at higher elevations (ca. 1,800 m) include at least five hylid (*Hyla chaneque*, *H. dendroscarta*, *H. mixe*, *Ptychohyla ignicolor*) and leptodactylid (*Eleutherodactylus* sp.) frogs and three species of plethodontid salamanders (*Nototriton adelos*, *Chiropterotriton* sp., *Thorius* sp.), all cloud-forest endemics. At the lower limit of its distribution, in the vicinity of Vista Hermosa (ca. 1,500 m elevation), *P. saltator* occurs with the same *Chiropterotriton*, a fully-webbed species of *Bolitoglossa* of the *rufescens-occidentalis* complex, a *Pseudoeurycea* tentatively identified as *P. werleri*, an unidentified species of *Thorius*, and at least seven species of hylids (*Agalychnis moreleti*, *Anotheca spinosa*, *Hyla arboreascandens*, *H. dendroscarta*, *H. echinata*, *Ptychohyla ignicolor*, *P. leonhardschultzei*).

In comparison with other members of the genus, *P. saltator* is active and fast-moving. The specific name *saltator* is Latin for leaper or dancer and refers to the unusual ability of this species to jump when attempting to elude capture. To our knowledge, the only other tropical plethodontids that combine rapid locomotion and well-developed jumping abilities are members of two recently discovered monotypic genera, *Nyctanolis* (Elias and Wake, 1983) and *Ixalotriton* (Wake and Johnson, 1989).

### *Pseudoeurycea parva* new species

Figure 4

**HOLOTYPE.** MVZ 196101, an adult male collected by Ken Lucas inside an arboreal bromeliad on a ridge SE Cerro Baul, 21 km W Rizo de Oro,



**Figure 4.** Photograph of a living *Pseudoeurycea parva* new species (MVZ 194330), collected at the type-locality.

Chiapas, Mexico (ca. 1,600 m). The type-locality is just within the eastern border of the state of Oaxaca.

**PARATYPES.** MVZ 196102, 196444–45 (3 specimens), 202294 (cleared and stained) same locality as holotype; MVZ 163823–25, 177823–24 (5 specimens), 16.8 km (by rd) NW Rizo de Oro (1,650–1,860 m); MVZ 194330–31 (2 specimens), Cerro Baul, 37 km (by rd) W Rizo de Oro; California Academy of Sciences (CAS) 164157–62 (6 specimens), Cerro Baul, 19 km W Rizo de Oro; LACM 137513, same locality as holotype.

**DIAGNOSIS.** This is the smallest known member of the genus. None of the 17 available specimens exceeds 40 mm SL, and all individuals with SL greater than 35 mm appear to be sexually mature. The combination of small size and a distinctive color pattern (brown dorsal stripe and lichenous white spots on the tail) easily separates this species from all other *Pseudoeurycea*, except *P. saltator*. Compared with the latter species, *P. parva* is smaller (median SL of the largest third of the sample = 39 mm in *P. parva* vs. 44 mm in *P. saltator*) and has a proportionately shorter tail (tail length projected to a common SL of 42 mm = 0.93 SL in *P. parva* vs. 1.02 SL in *P. saltator*). About half the specimens of *P. parva* lack a dorsal stripe, and when present the stripe is more obscure than in *P. saltator*. In the latter species, the dorsal pattern is formed by a heavily pigmented swath of iridophores; in contrast, the dorsal pattern of *P. parva* results from reduction in the density of melanin pigmentation in the mid-dorsal region. While *P. parva* lacks the diagnostic white tail tip found in *P. saltator*, most individuals possess conspicuous white or tan iridophore patches along the tail. There is often a pale patch on the rostrum.

In general appearance and ecology, *P. parva* somewhat resembles an oversized *Dendrotriton* (see also Wake and Elias, 1983) but differs from members of that genus in possessing prefrontal bones (see below, Osteology) and in lacking enlarged nostrils in both the juvenile and adult stages (Lynch and Wake, 1975). Both *P. parva* and *P. saltator* share some morphological and behavioral similarities with two recently discovered monotypic genera, *Nyctanolis* (Wake and Elias, 1983) and *Ixalo-*

*triton* (Wake and Johnson, 1989). However, the mosaic of similarities and differences argues against inclusion of *P. saltator* in either genus in the absence of more definitive evidence (see Discussion). We tentatively assign both new Oaxacan species to the genus *Pseudoeurycea* based on their generalized body proportions, configuration of the toes (middle digits are markedly longer than the outer ones), and retention of primitive skeletal features (see below, Osteology).

**MEASUREMENTS OF THE HOLOTYPE (mm).** Maximum head width, 6.4; head length, 9.3; depth at posterior angle of jaw, 3.1; eyelid length, 2.7; eyelid width, 1.5; anterior rim of orbit to snout, 2.9; interorbital distance, 2.5; distance between vomerine teeth and parasphenoid tooth patch, 0.1; snout to insertion of fore limb, 11.7; distance separating internal nares, 2.1; distance separating external nares, 2.4; snout projection beyond mandible, 0.9; snout to anterior angle of vent, 35.8; snout to posterior angle of vent (SL), 38.1; axilla to groin, 20.4; tail length, 38.9; tail width at base, 3.3; tail depth at base, 3.2; width of right hand, 3.1; width of right foot, 4.3; number of premaxillary teeth, 2; number of maxillary teeth, 80; number of vomerine teeth, 30.

**COLORATION OF THE HOLOTYPE IN ALCOHOL.** The ground color is dark gray-brown; the mid-dorsal region is lightened, forming an indistinct medium-brown stripe. The mid-dorsal stripe has a "dirty" appearance, due to a suffusion of small melanophores over unpigmented tissue. The dorsal stripe extends over the length of the tail, where it is overlain by large, scattered white iridophore patches. The belly is pale gray with scattered inconspicuous white flecks. Larger, more abundant white flecks are present in the lateral region of the trunk. The ventral surface of the tail is darker than the belly and has fewer iridophores. The chin is cream-colored, with a suffusion of tiny melanophores. The holotype, an adult male, possesses a well-developed kidney-shaped mental gland whose long axis is parallel to the anterior mandibular margin.

**VARIATION.** The dorsal ground color is dark brown or gray-brown in all specimens, but there is considerable individual variation in both the degree of development and the coloration of the mid-dorsal stripe. Some animals have a well-defined, contrasting stripe, others have only a slight reduction in the darkness of the ground coloration in the mid-dorsal region, and a few lack any dorsal pattern. Where present, the dorsal stripe varies in color from creamy white to dark brown, apparently depending on the degree of melanin reduction. Most individuals have at least a few conspicuous lichenous white spots scattered over the tail, but these spots vary in size and abundance. In general, individuals with reduced melanism in the mid-dorsal region also tend to be depigmented on the snout, parietal area, and limb bases. A suffusion of tiny white iridophores is invariably present on the ven-

ter, and somewhat larger white iridophores are concentrated in the lateral region of the trunk.

Sexual dimorphism is not evident in our limited sample, but there is statistically significant (determined according to methods of Lynch and Wake, 1975) ontogenetic variation in most proportional and meristic characters. Compared with standardized juveniles (character values projected to a common SL = 25 mm), standardized adults (projected to a common SL = 40 mm) have more maxillary + premaxillary teeth (80 vs. 60), more vomerine teeth (50 vs. 28), relatively longer limbs (combined length of fore limb and hind limb, divided by SL = 0.54 vs. 0.45), and relatively longer tails (tail length divided by SL = 0.91 vs. 0.62).

**OSTEOLOGY.** Information has been obtained from a cleared and stained adult female MVZ 202294 (40 mm SL). The skull is well developed, and the articulations are generally extensive and firm. The relatively stout premaxillary bone has a relatively broad, undivided pars dentalis that carries 6 bicuspid teeth. The latter are of moderate size (larger than the maxillary teeth) but are unspecialized in morphology. Frontal processes arise separately and remain separated, but they lie close together and enclose a narrow fontanelle. The processes are expanded distally, where they overlap the frontals in a firm articulation. The long and slender maxillary bones carry 32 and 33 small bicuspid teeth. These bones are rather firmly articulated to the premaxilla, the nasals, and the prefrontals. The nasals are broadly triangular in shape and of moderate size. Only a posterior tab overlaps the frontal. Septomaxillaries are absent. The prefrontals are somewhat elongate and articulate firmly with both the maxillaries and the frontals. Each prefrontal is about one-third the area of a nasal bone. The nasolacrimal duct passes between the nasal, prefrontal, and maxilla, and each bone is somewhat evacuated along the relevant margin, especially the prefrontal. Frontals and parietals are moderately ankylosed on the midline; there is only an extremely small frontal-parietal fontanelle. The parietal "spur" is only modestly developed, and there is no ventrally directed tab. Small lateral otic crests are present. Squamosals are notably large and are firmly articulated to the otic capsule. The vomers are barely ankylosed to each other posteriorly, and anteriorly the widely separated bones embrace a moderately large internasal fontanelle. Each of the long preorbital processes bears 13 teeth, which extend to the lateral margin of the internal nares. The posterior vomerine patches are narrow and well separated, and each bears about 45–50 small bicuspid teeth. The operculum bears a distinct, but very small, rod-like columella.

There is an atlas, 14 trunk vertebrae (13 of them rib-bearing), 1 sacral, 2 caudalsacral, and 30 caudal vertebrae. The first caudal vertebra is weakly specialized for tail autotomy. It is only slightly shorter than the neighboring vertebrae on each side, and its transverse processes are shorter than those on



Table 1. Samples used in electrophoretic study of proteins.

| Sample number | Species               | Locality                                           |
|---------------|-----------------------|----------------------------------------------------|
| 1             | <i>P. brunnata</i>    | San Marcos, Guatemala                              |
| 2             | <i>P. goebeli</i>     | San Marcos, Guatemala                              |
| 3             | <i>P. juarezi</i>     | 52 km NE Guelateo, Oaxaca, Mexico                  |
| 4             | <i>P. rex</i>         | San Marcos, Guatemala                              |
| 5             | <i>P. rex</i>         | Cerro Mozotal, Chiapas, Mexico                     |
| 6             | <i>P. smithi</i>      | Cerro San Felipe, Oaxaca, Mexico                   |
| 7             | <i>D. bromeliacia</i> | San Marcos, Guatemala                              |
| 8             | <i>N. pernix</i>      | Finca Chiblac, Huehuetenango, Guatemala            |
| 9             | <i>I. niger</i>       | 12 km N Berriozabal, Chiapas, Mexico               |
| 10            | <i>P. saltator</i>    | 65 km NE Guelateo, Oaxaca, Mexico                  |
| 11            | <i>P. parva</i>       | Cerro Baul, 16.8 km NW Rizo de Oro, Oaxaca, Mexico |

the first few caudal vertebrae, an unusual condition. Transverse processes of the first caudal vertebra are only slightly swept forward from near the anterior end of the vertebra. Transverse processes are distinct on all but the last two, tiny caudal vertebrae.

The hands and feet are typical for *Pseudoeurycea*, except that there is no sign of a tibial spur. Terminal phalanges have moderate distal expansion (Fig. 3).

The hyobranchial apparatus is generally typical of the genus, but there is a distinct, well-developed lingual cartilage on the basibranchial.

**RANGE.** *Pseudoeurycea parva* has been collected only on and around Cerro Baul, a relatively isolated 2,000-m peak that lies along the continental divide just east of the Isthmus of Tehuantepec (Fig. 1). The cluster of known localities is in easternmost Oaxaca, 5–10 km west of the state border with Chiapas. Access to the area is from Chiapas, via the Pan-American highway and a rough track from the settlement of Rizo de Oro. Topographic maps indicate the existence of poorly explored montane areas, some of them higher and more extensive than Cerro Baul, just west of the type-locality. Assuming these uplands also support cloud forest, *P. parva* may have a somewhat larger range than present records indicate. Nevertheless, the low-lying, subhumid Isthmus of Tehuantepec, less than 25 km W of Cerro Baul, constitutes a major distributional barrier (Fig. 1). East of the type-locality, elevations drop below 1,500 m for nearly 50 km, before rising to 2,000 m at Cerro Tres Picos, near Tonalá, Chiapas. The salamander fauna at Cerro Tres Picos includes an endemic *Dendrotriton* (*D. megarhinus*) and an undescribed large *Bolitoglossa* of the *franklini* species-group (Wake and Lynch, 1982), but *P. parva* has not been found there.

**HABITAT AND HABITS.** All specimens of *P. parva* have been collected inside arboreal bromeliads within cloud forest at elevations ranging from 1,500 to 1,900 m. The large tank-type bromeliads used by the species have been identified as species of *Vriesia* and *Tillandsia* (D. Breedlove, pers. comm.). The only other salamander reported from Cerro Baul, a small *Bolitoglossa* of the *rufescens*-

*occidentalis* group, also occurs inside arboreal bromeliads. The specific name *parva* is a Latin word meaning small.

PROTEIN COMPARISONS

METHODS

Both *P. parva* and *P. saltator* are distinctive morphologically, and their recognition as valid species does not depend on biochemical data. However, we have employed starch-gel electrophoresis of proteins as an independent means for assessing the degree of genetic differentiation of the two new species. In the future we hope to address problems of paraphyly (and possibly polyphyly) within *Pseudoeurycea* (Wake and Lynch, 1976; Maxson and Wake, 1981; Wake and Elias, 1983). Here, we consider three narrower questions. (1) Are *P. saltator* and *P. parva* close phyletic relatives? (2) Which other species of *pseudoeurycea* are most closely related to the two new species? (3) Does discovery of *P. parva* and *P. saltator* provide insight into the cladistic relationships among *Pseudoeurycea*, *Ixalotriton*, *Nyctanolis*, and *Dendrotriton*?

The procedures we employed for study of proteins have been described in detail elsewhere (Lynch *et al.*, 1977, 1983; Wake and Lynch, 1982). Briefly, we used horizontal starch-gel electrophoresis to analyze variation in 13 proteins in the two new species and in five described species of *Pseudoeurycea* (*P. brunnata*, *P. goebeli*, *P. juarezi*, *P. rex*, *P. smithi*), one species of *Dendrotriton* (*D. bromeliacia*), *Nyctanolis pernix*, and *Ixalotriton niger* (Table 1). An additional four proteins were analyzed for some taxa. Only two specimens from each population were used for most comparisons. The various taxa are sufficiently well differentiated that even small samples should provide useful information (Gorman and Renzi, 1979). Indeed, they are so distant from one another cladistically that they have few similarities, and even these should be considered suspect. A practical difficulty is that so many cross comparisons are required that tissue extracts are often exhausted before questions of protein identity are resolved.



Table 2. Proteins and conditions of analysis.

| Enzyme                             | Enzyme<br>commis-<br>sion<br>number | Locus    | Buffer                        | Voltage and<br>time run |
|------------------------------------|-------------------------------------|----------|-------------------------------|-------------------------|
| Phosphogluconate dehydrogenase     | 1.1.1.44                            | pgdh     | Tris maleate with NADP in gel | 100 V (3.5 h)           |
| Adenosine deaminase                | 3.5.4.4                             | ada      | Tris maleate with NADP in gel | 100 V (3.5 h)           |
| Glycerol-3-phosphate dehydrogenase | 1.1.1.8                             | gpd      | Tris maleate with NADP in gel | 100 V (3.5 h)           |
| Isocitrate dehydrogenase           | 1.1.1.42                            | icdh-1,2 | Tris citrate, pH 8.0          | 130 V (4 h)             |
| Mannose phosphate isomerase        | 5.3.1.8                             | mpi      | Tris citrate, pH 8.0          | 130 V (4 h)             |
| Iditol dehydrogenase               | 1.1.1.14                            | iddh     | Tris citrate, pH 8.0          | 130 V (4 h)             |
| Phosphoglucomutase                 | 2.7.5.1                             | pgm-1,2  | Tris citrate, pH 8.0          | 130 V (4 h)             |
| Phosphoglucose isomerase           | 5.3.1.9                             | pgi      | Tris citrate, pH 7.0          | 180 V (3 h)             |
| Leucine aminopeptidase             | 3.4.11.1                            | lap      | Tris citrate, pH 7.0          | 180 V (3 h)             |
| Malate dehydrogenase               | 1.1.1.37                            | mdh-1,2  | Tris citrate, pH 7.0          | 180 V (3 h)             |
| Aspartate aminotransferase         | 2.6.1.1                             | aat      | LiOH                          | 300 V (3 h)             |
| Tripeptide aminopeptidase          | 3.4.11.4                            | pep-b    | LiOH                          | 300 V (3 h)             |
| Dipeptidase                        | 3.4.13.11                           | pep-c    | LiOH                          | 300 V (3 h)             |
| Lactate dehydrogenase              | 1.1.1.27                            | ldh      | Poulik                        | 250 V (3 h)             |

RESULTS

The comparison of 13 proteins yielded 70 presumptive genetic alleles ( $x = 5.4$  per locus); the comparison of 17 proteins yielded 101 alleles ( $x = 5.9$  per locus), but there were difficulties in accu-

rately scoring the four additional proteins in some samples. The following discussion is based on the results of the more reliable 13-locus study, except where otherwise noted (Tables 2 and 3). We fully realize that this is too low a number of proteins to be of critical value in determining phylogenetic pat-

Table 3. Allele frequencies for 13 allozyme loci. Lowercase letters in the body of the table refer to electrophoretically distinguishable alleles. For abbreviations see Table 2.

| Species sample number (see Table 1) |              |                                     |                        |                        |                                     |              |              |
|-------------------------------------|--------------|-------------------------------------|------------------------|------------------------|-------------------------------------|--------------|--------------|
| Locus                               | 1<br>(n = 2) | 2<br>(n = 2)                        | 3<br>(n = 2)           | 4<br>(n = 2)           | 5<br>(n = 3)                        | 6<br>(n = 2) | 7<br>(n = 2) |
| pgdh                                | d (1.00)     | b (1.00)                            | c (0.250)<br>d (0.750) | c (0.750)<br>d (0.250) | c (0.333)<br>d (0.667)              | b (1.00)     | e (1.00)     |
| icdh-1                              | c (1.00)     | h (0.750)<br>i (0.250)              | f (1.00)               | g (0.750)<br>h (0.250) | h (0.333)<br>i (0.667)              | d (1.00)     | a (1.00)     |
| icdh-2                              | a (1.00)     | b (1.00)                            | b (1.00)               | b (1.00)               | b (1.00)                            | a (1.00)     | a (1.00)     |
| mpi                                 | b (1.00)     | b (1.00)                            | a (0.250)<br>b (0.750) | c (1.00)               | a (0.167)<br>b (0.833)              | b (1.00)     | d (1.00)     |
| iddh                                | d (1.00)     | e (1.00)                            | b (1.00)               | e (1.00)               | c (1.00)                            | e (1.00)     | e (1.00)     |
| pgm-1                               | b (1.00)     | d (1.00)                            | c (1.00)               | b (1.00)               | b (1.00)                            | b (1.00)     | b (1.00)     |
| pgm-2                               | c (1.00)     | d (1.00)                            | b (1.00)               | c (1.00)               | c (1.00)                            | c (1.00)     | c (1.00)     |
| pgi                                 | d (1.00)     | d (1.00)                            | a (0.250)<br>b (0.750) | d (1.00)               | d (1.00)                            | d (1.00)     | b (1.00)     |
| lap                                 | c (1.00)     | d (1.00)                            | a (0.250)<br>c (0.750) | c (1.00)               | c (1.00)                            | b (1.00)     | f (1.00)     |
| aat                                 | e (1.00)     | f (1.00)                            | e (1.00)               | f (1.00)               | f (1.00)                            | e (1.00)     | c (1.00)     |
| pep-b                               | b (1.00)     | a (0.250)<br>c (0.750)              | c (0.750)<br>d (0.250) | b (1.00)               | b (1.00)                            | b (1.00)     | c (1.00)     |
| pep-c                               | b (1.00)     | c (0.250)<br>e (0.500)<br>g (0.250) | c (1.00)               | d (0.500)<br>f (0.500) | c (0.667)<br>e (0.167)<br>g (0.167) | e (1.00)     | g (1.00)     |
| ldh                                 | c (1.00)     | c (1.00)                            | b (0.250)<br>c (0.750) | f (1.00)               | e (1.00)                            | c (1.00)     | b (1.00)     |

terns. However, the data demonstrate the distinctiveness of the species and serve to generate hypotheses of relationship. For practical reasons of comparison with the now-extensive literature on protein evolution in salamanders, we present Nei genetic distances, but we recognize that at the levels of differentiation we have found, any distant measure has little reliability as an exact measure.

The smallest value in the genetic distance matrix ( $D_N = 0.3$ ; 3 fixed allelic differences) separates two geographically isolated populations of *P. rex*. The smallest  $D_N$  value for between-species comparisons ( $D_N = 0.5$ ; 5 fixed allelic differences) separates *P. brunnata* and *P. smithi*. At the opposite extreme, several values exceed  $D_N = 1.5$ , the maximum being 4.1 (12 fixed allelic differences) between *P. goebeli* and *P. parva*. The degree of genetic differentiation between *P. parva* and *P. saltator* ( $D_N = 0.8$ ; 6 fixed allelic differences) is substantial in comparison to other salamander genera (Highton and Larson, 1979; Larson, 1984; Larson et al., 1981). In the 17-locus comparison, the degree of differentiation between *P. parva* and *P. saltator* increases to  $D_N = 1.0$ , with 10 of 17 loci having apparent fixed allelic differences. The proteins we examined of the two new species are more similar to one another than they are to any other species of *Pseudoeurycea* or to the other genera included in our comparison.

Table 3. Extended.

| Species sample number  |                        |                        |                        |
|------------------------|------------------------|------------------------|------------------------|
| 8<br>(n = 2)           | 9<br>(n = 2)           | 10<br>(n = 2)          | 11<br>(n = 2)          |
| f (1.00)               | a (1.00)               | c (1.00)               | a (1.00)               |
| b (1.00)               | e (1.00)               | f (1.00)               | b (1.00)               |
| a (1.00)               | a (1.00)               | c (1.00)               | a (1.00)               |
| d (1.00)               | b (1.00)               | a (1.00)               | a (0.500)<br>c (0.500) |
| a (1.00)               | c (1.00)               | d (1.00)               | d (1.00)               |
| d (1.00)               | a (0.500)<br>b (0.500) | b (1.00)               | b (1.00)               |
| d (1.00)               | a (1.00)               | a (1.00)               | a (1.00)               |
| c (1.00)               | b (1.00)               | b (1.00)               | b (1.00)               |
| f (1.00)               | d (1.00)               | e (1.00)               | b (1.00)               |
| a (1.00)               | a (1.00)               | b (1.00)               | b (0.750)<br>d (0.250) |
| c (0.500)<br>d (0.500) | c (1.00)               | c (1.00)               | c (0.750)<br>d (0.250) |
| c (1.00)               | a (1.00)               | c (1.00)               | a (0.250)<br>b (0.750) |
| a (1.00)               | b (1.00)               | b (0.750)<br>d (0.250) | a (1.00)               |

Other than *P. saltator*, the species of *Pseudoeurycea* most similar to *P. parva* is *P. brunnata* ( $D_N = 1.0$ ; 8 fixed allelic differences); relative to *P. saltator*, the most similar species other than *P. saltator* is *P. juarezi* ( $D_N = 1.0$ ; 10 fixed allelic differences). There is substantial asymmetry in these results in that *P. saltator* is much more differentiated from *P. brunnata* ( $D_N = 1.9$ ; 11 fixed allelic differences) than is *P. parva*. Conversely, *P. parva* is more highly differentiated from *P. juarezi* ( $D_N = 2.3$ ; 10 fixed allelic differences) than is *P. saltator*.

The two species that are least differentiated from *Ixalotriton* are *P. parva* ( $D_N = 0.9$ ; 6 fixed allelic differences) and *P. saltator* ( $D_N = 1.1$ ; 8 fixed allelic differences). *Nyctanolis* is more similar to *Ixalotriton* ( $D_N = 1.3$ ; 9 fixed allelic differences) than are the remaining species of *Pseudoeurycea* in our sample. However, the species most similar to *Nyctanolis* is *P. parva* ( $D_N = 1.1$ ; 9 fixed allelic differences), followed by *Ixalotriton*, then a group of 4 species of *Pseudoeurycea*, including *P. saltator* ( $D_N = 1.5$ – $1.6$ ). *Dendrotriton* differs substantially from all other taxa (minimum  $D_N = 1.4$ ).

DISCUSSION

As currently constituted, the genus *Pseudoeurycea* is a taxonomic category of convenience. Its species, many of which are rather generalized in morphology, share no uniquely derived osteological traits. Instead, the species assigned to *Pseudoeurycea* are characterized mainly by their lack of the derived traits that define other plethodontid genera (Wake and Elias, 1983). Electrophoretic analysis of proteins (Lynch et al. 1977, 1983; data presented herein; unpubl. data) and immunological studies (Maxson and Wake, 1981) indicate the existence of ancient phyletic divisions within *Pseudoeurycea*, but difficulties in obtaining fresh specimens of key taxa have made comprehensive biochemical comparisons impossible. In addition, few, if any, morphological traits are unambiguously correlated with biochemical patterns of similarity. Finally, there are a number of undescribed species that may affect the construction of new generic or subgeneric categories, as well as nominal species (e.g., *P. bellii*) that may constitute species groups.

Several species that may be related to *Pseudoeurycea* have been assigned to new genera (*Ixalotriton*, *Nyctanolis*, *Dendrotriton*) on the basis of a few rather accentuated morphological differences that may not accurately reflect cladistic relationships. Some species-groups of *Pseudoeurycea* (*sensu lato*) may be closer cladistically to these genera than they are to each other (Maxson and Wake, 1981). Our protein data suggest the possibility that one or both of the two new species may be closer to *Ixalotriton* or *Nyctanolis* than to at least some other species of *Pseudoeurycea*.

Comparative osteological information provides conflicting indications of relatedness. For example, *Dendrotriton* differs from some *Pseudoeurycea* (in-

cluding the two new species) and from *Ixalotriton* and *Nyctanolis* in having septomaxillae (a plesiomorphic trait also found in certain species of *Pseudoeurycea*; see Wake and Elias, 1983), and from all species of these genera in lacking prefrontals and having large nostrils as juveniles and large openings of the olfactory sac throughout life (synapomorphies). *Nyctanolis* has divided premaxillary bones, an attached lingual cartilage, and tibial spurs, all plesiomorphic traits. All other genera of tropical plethodontid salamanders have a single premaxillary bone, a synapomorphy (Elias and Wake, 1983). Free lingual cartilages (an apomorphy) are found in *Ixalotriton*, *Dendrotriton*, and some *Pseudoeurycea*, including *P. parva*, but lingual cartilages are absent (another apomorphy that may be derived from the free lingual cartilage or may be independent of it) in other *Pseudoeurycea*, including *P. saltator*. Tibial spurs are present in most species of *Pseudoeurycea*, including *P. saltator*, but are absent (an apomorphy) in *Dendrotriton*, *Ixalotriton*, and *P. parva*. In one very specialized and apomorphic trait, the possession of enlarged, hook-like premaxillary teeth (Taylor, 1941), *P. saltator* differs from *P. parva* and all other neotropical salamanders except *P. smithi* and *P. unguidentis*, two species from northern Oaxaca.

Thus, while the protein evidence favors a hypothesis of relatively close relationship between the two new species, the morphological evidence suggests that *P. saltator* is clearly aligned with *Pseudoeurycea*, whereas *P. parva* is more isolated cladistically. The latter species may be more closely related to species currently assigned to other genera (e.g., *Ixalotriton*) than to the remainder of the genus *Pseudoeurycea*.

The group of species and genera considered here may represent cladistic fragments of a basal radiation in the supergenus *Bolitoglossa*. The deep genetic differentiation of the group and the ambiguous nature of the morphological data suggest a complex pattern of mosaic evolution. As a result, it is impossible to present a well-supported cladistic hypothesis at the present time.

## HISTORICAL BIOGEOGRAPHY

Recent discoveries of new salamander species and genera in southeastern Mexico and adjacent Guatemala (e.g., Lynch and Wake, 1975, 1978; Wake and Lynch, 1982; Elias and Wake, 1983; Wake and Elias, 1983; Elias, 1984; Wake and Papenfuss, 1987; Wake and Johnson, 1989), and systematic revision of known genera (Wake and Elias, 1983), have strengthened our earlier conclusion (Wake and Lynch, 1976) that the mountains of nuclear Central America and the adjacent highlands of Oaxaca are major evolutionary centers for neotropical plethodontids. However, we previously emphasized the importance of the relatively young (Pliocene-Pleistocene) volcanic highlands of nuclear Central America as centers of species proliferation (Wake

and Lynch, 1976), whereas it has become increasingly evident that the ancient (pre-Cretaceous) geologic core of the region has been the site of a much older and more profound phyletic radiation. Since 1976, four new plethodontid genera (*Bradytriton*, *Dendrotriton*, *Ixalotriton*, *Nyctanolis*) have been discovered to be endemic to a limited area of ancient mountains in Chiapas and adjacent Guatemala; five other widespread plethodontid groups (*Bolitoglossa*-alpha, *Bolitoglossa*-beta, *Nototriton*, *Oedipina*, *Pseudoeurycea*) occur in the same region, which thus contains representatives of all generic groups of plethodontids that occur anywhere in nuclear Central America (Wake and Lynch, 1976; Wake and Elias, 1983). Only the Orizaba region of Veracruz, Mexico, with seven generic-level groups (*Bolitoglossa*-alpha, *Bolitoglossa*-beta, *Pseudoeurycea*, *Chiropterotriton*, *Lineatriton*, *Parvimolge*, *Thorius*) approaches the generic diversity of the plethodontid fauna of eastern Chiapas and western Guatemala. Although the precipitous Atlantic slope of Oaxaca, where *P. saltator* occurs, lies between these two major centers of endemism and diversity, the Atlantic highlands of Oaxaca are separated from nuclear Central America by the low-lying, sub-humid Isthmus of Tehuantepec. The mountains of northern Oaxaca are rich in endemic plethodontid species (Wake, 1987; Wake *et al.*, 1988), but the salamander fauna of the area is not distinctive at the generic level; five of the six generic groups that occur in northern Oaxaca (*Bolitoglossa*-alpha, *Bolitoglossa*-beta, *Pseudoeurycea*, *Chiropterotriton*, *Thorius*) also are found in the Orizaba region. The sole exception is the recently described *Nototriton adelos* Wake and Papenfuss, 1987, whose affinities lie to the southeast, in nuclear Central America.

Despite earlier views that the Isthmus of Tehuantepec was the locus of a Tertiary marine portal (e.g., Stuart, 1966), geologists now believe the area has been land-positive since at least the Cretaceous (Malfait and Dinkelman, 1972). Nevertheless, the isthmian region must have formed a long-standing distributional barrier for animals that require cool, humid conditions (Halffter, 1987). Two lowland species of *Bolitoglossa* (*B. mexicana*, *B. rufescens*) occur on both sides of the Isthmus, but no montane species does so. Indeed, the only species-groups of high-elevation salamanders with representatives east and west of the Isthmus are the *gadovii* group of *Pseudoeurycea* (*sensu* Maxson and Wake, 1979) and, possibly, two recently described species of *Nototriton* (Papenfuss and Wake, 1987). Apart from *P. parva*, just five species of *Pseudoeurycea* range east of the Isthmus of Tehuantepec: *P. brunnnata*, *P. expectata*, *P. goebeli*, *P. rex*, and an undescribed Guatemalan species (Wake and Lynch, 1976). All are found at high elevations (above 2,500 m) in Guatemala and easternmost Chiapas, usually in terrestrial microhabitats. Our analysis of protein data suggests that this assemblage is only distantly related to *P. saltator* and *P. parva*.

Both *P. parva* and *P. saltator* have ambiguous



relationships to other *Pseudoeurycea* and to allied genera. *Pseudoeurycea parva* resembles *Dendrotriton* in habitus, and is intermediate in overall size between the largest *Dendrotriton* and the next smallest *Pseudoeurycea*. The habitat/microhabitat association of *P. parva* (arboreal bromeliads in mid-elevation cloud forests) is typical of *Dendrotriton* (Wake and Lynch, 1976; Lynch and Wake, 1975, 1978) but unusual in *Pseudoeurycea*, most species of which inhabit terrestrial microhabitats at high elevations (Wake and Lynch, 1976). Three allopatric *Dendrotriton* (*D. bromeliacia*, *D. xoloccalcae*, *D. megarhinus*) occupy the three known isolates of montane cloud forest along the Pacific versant between western Guatemala and the range of *P. parva*, a fact consistent with the hypothesis that both groups comprise remnants of a once continuous range. On the Atlantic versant, the ecological roles of *Dendrotriton* and *P. parva* are filled by *D. rabbi* in west-central Guatemala, *Nyctanolis* in western Guatemala and adjacent Chiapas, *Ixalotriton* in central Chiapas, and *P. saltator* in central Oaxaca. Again, the fact that none of the eight species of small to medium-sized arboreal specialists are sympatric is consistent with the hypothesis that a breakup of formerly continuous areas of cloud forest stranded ancestors of these salamanders within isolated areas of favorable habitat on the margins of the ancient core of nuclear Central America.

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